Conodont biostratigraphy of the Uppermost Ordovician and Lowermost Silurian

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Synopsis

A review of the conodont biostratigraphy of the Ordovician–Silurian boundary sections in North America, Europe, and Asia shows that virtually all sections are either incomplete stratigraphically or have intervals from which no diagnostic conodonts are known. The best known conodont succession across the systemic boundary is on Anticosti Island, where, however, the precise level of the boundary remains unknown because of the absence of diagnostic graptolites. Ordovician and Silurian conodont faunas differ greatly and there is conclusive evidence that a conspicuous turnover in the conodont faunas took place globally in the systemic boundary interval. This turnover involved the replacement of a fauna of Ordovician aspect containing more than 25 genera with one of Silurian aspect having fewer than 15 genera, eight of which are known also from the Ordovician. A few coniform conodont species survived this extinction event, but we have identified only one species with compound elements in the apparatus that may range from the uppermost Ordovician to lowermost Silurian; however, even in the case of this form, there is some question whether we are dealing with the same species in both systems. The dating of the conodont faunal turnover in terms of standard graptolite zones is still somewhat uncertain, but available data suggest that it occurs in an interval in the upper *G. persculptus* Zone but below the systemic boundary. This extinction event is probably a result of the Saharan glaciation. In those cases where the origin of the Llandovery stocks is known or can be postulated, they appear to be derived, in almost all cases, from stocks that inhabited the tropical waters of the Midcontinent Province during the Ordovician. It is concluded that further studies are urgently needed, particularly to date exactly the conodont faunal turnover and to define the Ordovician–Silurian boundary in terms of the conodont succession.

Introduction

Extensive research during the last few decades has firmly established conodonts as a key zone fossil group in Ordovician and Silurian rocks. The conodont zone successions now in use within each of these systems provide a stratigraphical resolution which in many cases is superior to that of other fossil groups, also including the graptolites. Furthermore, the fact that conodonts are present in rocks representing the whole range of marine depositional environments from basinal to intertidal, or even supratidal, makes them very useful for both local and regional biostratigraphical work. This is particularly the case in the shallow-water carbonate deposits that occupy vast areas on the cratons of all continents except Africa and Antarctica but which contain only few and scattered occurrences of zonal graptolites.

In view of the significance of conodonts as zonal fossils in Ordovician–Silurian strata, it is hardly surprising that they played a major role in the lengthy discussions about the Ordovician–Silurian boundary which were carried out within the Ordovician–Silurian Boundary Working Group of the I.U.G.S Commission on Stratigraphy. Although it was ultimately decided to define this systemic boundary on graptolites, the absence of diagnostic graptolites in many boundary sections, particularly the cratonic ones, makes it necessary to use other fossils for establishing the precise level of the systemic boundary. Conodonts have great potential to serve in this capacity. The purpose of the present contribution is to summarize and assess currently available conodont evidence that has bearing on the recognition and definition of the Ordovician–Silurian boundary. Although we attempt global coverage, we will concentrate on North America and Europe, where the most detailed studies have been carried out and from which we have not only easily accessible information but also personal field experience of most of the important boundary sections.

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Upper Ordovician–Lower Silurian Conodont Zonations

The striking faunal provincialism of Late Ordovician conodonts (Barnes *et al.* 1973; Bergström 1973; Sweet & Bergström 1974, 1984; Dzik 1983) has necessitated the use of separate biostratigraphical zonal schemes for the North Atlantic and Midcontinent provinces. Although Sweet & Bergström (1984) recently introduced more refined provincial units for the Upper Ordovician of North America and Europe, in the present contribution, which is global in scope, we use only these two provinces. Provincialism was not conspicuous during the Early Silurian but several slightly different zonal schemes have been proposed. However, eventually it may be possible to use a single zonal scheme globally for this part of the succession.

The Middle and Upper Ordovician zone succession for the North Atlantic Province developed by Bergström (1971*a*, 1971*b*, 1978, 1983, 1986) has been tested and used by many other authors, e.g. Dzik (1976, 1983), Harris *et al.* (1979), Orchard (1980), and Schönlaub (1971, 1980). This zonal scheme (Fig. 1) is based on the evolutionary lineage of *Amorphognathus*. The successive zones of *A. tvaerensis*, *A. superbus*, and *A. ordovicicus* covers the Caradoc–Ashgill interval. The *A. tvaerensis* Zone has three named subzones but no attempt has yet been made to subzone the *A. superbus* and *A. ordovicicus* Zones although the restricted stratigraphical range of some taxa (e.g. *A. complicatus*, *Hamarodus europaeus*, *Sagittodontina robusta*; Bergström 1983: fig. 1) may eventually allow this (cf. Orchard 1980).

Conodont biostratigraphical classification of the Upper Ordovician of the Midcontinent Province was first developed as a sequence of faunas characteristic of particular stratigraphical intervals (Sweet *et al.* 1971; Sweet & Bergström 1976; McCracken & Barnes 1981). The interval of Faunas 10–13 covered the Cincinnatian Series. Later work by Sweet (1979*a*, 1979*b*, 1984) using graphic correlation methods has led to the establishment of a Composite Standard Section and a formal zonal scheme with the successive *Belodina confluens*, *Oulodus velicuspis*, *O. robustus*, *Aphelognathus grandis*, *A. divergens*, and *A. shatzeri* Zones. Because of regional migration of North Atlantic Province faunal elements into the Midcontinent Province during the Late Ordovician (Sweet *et al.* 1971: fig. 3), it is possible to tie some of the zonal boundaries of these two provincial zone schemes (Sweet 1984: fig. 2). Other studies documenting and supporting this scheme include those of Nowlan & Barnes (1981), McCracken & Barnes (1981, 1982) and Nowlan *et al.* (in press). Outside North America, studies of cratonic conodont faunas have been undertaken by, among others, Moskalenko (1983), An (1981), and An *et al.* (1983), and a formal zonation has been proposed for Siberia (Moskalenko 1983). It is possible that other low latitude Ordovician plates (e.g. Kazakhstan, north China and Australia) may require separate zonal schemes because their conodont faunas include many endemic elements.

The first attempt to develop a conodont zonal scheme for the Lower Silurian was by Walliser (1964, 1971) from work in the Carnic Alps. Work in this area was later undertaken by Schönlaub (1971, 1980). Following descriptions of faunas from other regions, it gradually became apparent that the Carnic Alps standard sequences were stratigraphically incomplete. Aldridge (1972, 1975) established a new zonation in the Welsh Borderland, but non-productive clastics in the lowermost Silurian there prevented the establishment of a complete zonal succession through the Llandovery. In North America, Barrick (1977), Barrick & Klapper (1976), Cooper (1975, 1980), Fåhraeus & Barnes (1981), Helfrich (1980), LeFèvre *et al.* (1976), McCracken & Barnes (1981), Nowlan (1983), Pollock *et al.* (1970), Rexroad (1967), Nicoll & Rexroad (1971), and Uyeno & Barnes (1983), among others, have documented faunas from important sequences. Elsewhere, studies of Early Silurian conodonts include those of Männik (1983) in Severnaya Zemlya, USSR, Lin (1983) in China, and Igo & Koike (1968) from Malaysia.

As a result of these studies, two Lower Silurian conodont zone schemes have evolved for North America and Europe (Fig. 1) and another for China. However, the phylogenies of important lineages, such as those of *Icriodella*, *Distomodus* and *Oulodus*, have yet to be fully documented, and the precise ranges of several key species, including platform taxa, are not yet established. Once these have been clarified, particularly in sequences such as those on Anticosti Island, a single zonal scheme should be applicable to most areas. There is also an urgent need for further documentation of the conodont species succession across the Ordovician–Silurian

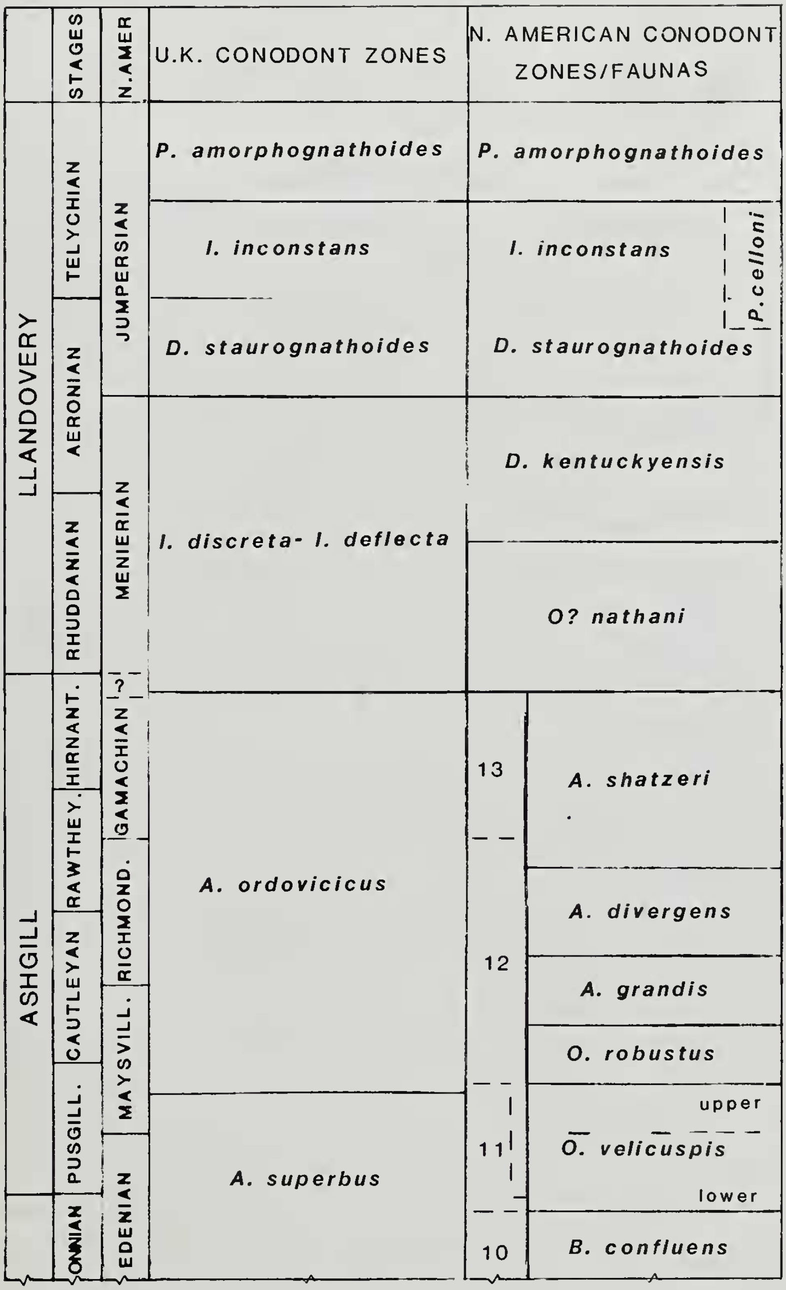

Fig. 1 Late Ordovician–Early Silurian chronostratigraphy and conodont zonation for U.K. and North America. For new terminology of Silurian chronostratigraphy see Barnes (in press) and Holland (1985); for zones see references in text.

boundary. Even though faunal provincialism is much reduced in the Lower Silurian when compared to the Upper Ordovician, the conodont faunas exhibit considerable differentiation horizontally; hence there are significant biofacies differences between nearshore and basinal environments (e.g. Aldridge & Mabillard 1981), and community patterns across shelf environments can be deduced (e.g. LeFèvre *et al.* 1976; McCracken & Barnes 1981; Nowlan 1983; Uyeno & Barnes 1983).

North America

Conodont studies of strata close to, or across, the boundary interval have been undertaken in many regions in North America, including Anticosti Island, Gaspé, the Michigan, Hudson Bay, Williston and Illinois basins and adjoining arch areas, the western Midcontinent, the Cordillera, Arkansas–Oklahoma, and the Canadian Arctic and its extension into northern Greenland. The best section currently known is on Anticosti Island, Québec, where there is a continuous and continuously fossiliferous sequence across the systemic boundary. Elsewhere, there is a stratigraphical hiatus in the boundary interval, or the faunal sequence is incomplete.

The Anticosti Island conodont sequence (Fig. 2) has been documented by Nowlan & Barnes (1981), McCracken & Barnes (1981), Fåhraeus & Barnes (1981), Uyeno & Barnes (1983), and Barnes (this volume). Conodont Fauna 13 is developed in Gamachian strata, and the *Oulodus*? *nathani*, *Distomodus kentuckyensis*, *D. staurognathoides*, *Icriodella inconstans*, and *Pterospathodus amorphognathoides* Zones (Fig. 1) are recognized in Llandovery strata. These studies are based on intensive sampling and on the investigation of nearly 100 000 superbly preserved conodonts. Conodont Fauna 13 of McCracken & Barnes (1981), which contains the distinctive genus *Gamachignathus*, is associated with Ordovician macrofossils such as *Vellamo* and aulacerids. Through the overlying *O.*? *nathani* Zone there is a sequential occurrence of Silurian brachiopods (*Zygospiraella*, *Stricklandia*, *Virgiana*) and the trilobite *Acernaspis* (Lespérance 1985). From one locality on eastern Anticosti Island Cocks & Copper (1981) reported a *Hirnantia* brachiopod fauna just below a level where Nowlan (1982) recovered conodonts of Silurian aspect.

On the Gaspé Peninsula (Fig. 2), Québec, the White Head Formation exhibits a faunal sequence similar to that of Anticosti Island. *Gamachignathus* (Fauna 13) is known from Unit 4 of this formation, the *Hirnantia* fauna and the *Mucronaspis* fauna are well developed and associated with *G. persculptus* Zone graptolites in Unit 5, and *Acernaspis* occurs with Silurian conodonts (*D. kentuckyensis*) in Unit 6 (Nowlan 1981, 1983; Lespérance 1985). In another part of Gaspé, the *O.*? *nathani* Zone has been recognized in the Clemville Formation (Nowlan 1983).

On Anticosti Island there is a marked faunal change with a rapid replacement of a diverse Ordovician conodont fauna with a distinctive, but less diverse, Silurian fauna. In an interval up to two metres thick, a few Ordovician taxa co-occur with species of Silurian aspect. Unfortunately, the absence of graptolites diagnostic of the *P.*? *acuminatus* Zone in the Anticosti Island succession makes it impossible to establish the precise level of the systemic boundary, and the relations between the faunal turnover and this level. The fact that the uppermost interval of Fauna 13 has a *Hirnantia* fauna and graptolites of the *G. persculptus* Zone on Gaspé (Lespérance 1985) shows that the conodont fauna below the turnover interval is of pre-Silurian age, and the systemic boundary must be at a higher stratigraphical level in Anticosti. Lespérance (1985) suggested that the appearance of *Acernaspis* may be coeval with the base of the *P.*? *acuminatus* Zone and hence mark the systemic boundary; however, as noted below, the reliability of the appearance of this genus regionally as a guide to the boundary level needs confirmation, and its appearance on Anticosti Island might be at a higher stratigraphical level than in some other areas.

In Ontario and Michigan in the Great Lakes region, conodont studies have revealed the existence of a hiatus at the boundary that spans the Gamachian Stage and possibly parts of the Richmondian and early Llandovery as well (cf. Barnes & Bolton, this volume). Fauna 13 and the *O.*? *nathani* Zone are not recognized in this area. A similar hiatus exists to the north in the Hudson Bay Basin (LeFèvre *et al.* 1976) and to the south in the Cincinnati Region (cf. Sweet

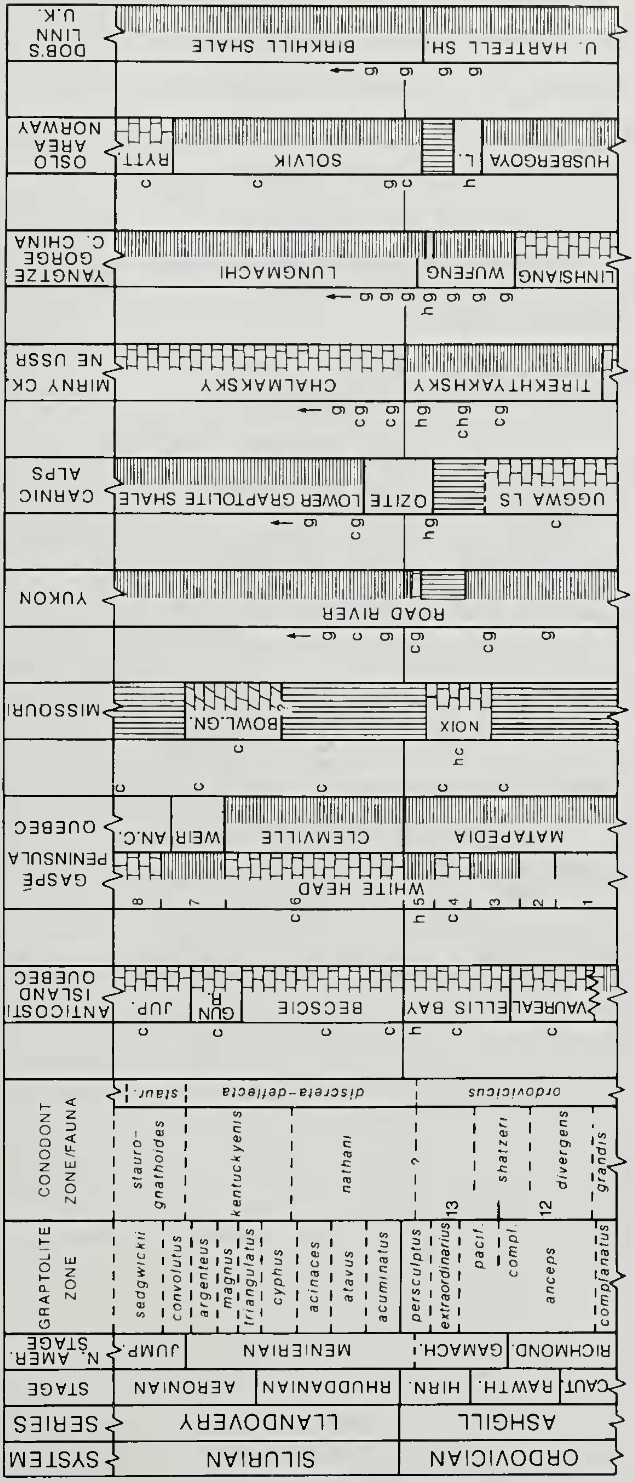

Fig. 2 Key stratigraphical sections across the Ordovician–Silurian boundary showing dominant lithologies of formation and their biostratigraphical correlation based on presence of conodont (c), graptolite (g), and *Hirnantia* (h) faunas.

1979*a*, 1984; Grahn & Bergström 1985). The faunas of the latter region have been well documented in the last decades by W. C. Sweet and co-workers for the Ordovician and C. B. Rexroad and co-workers for the Llandovery. Further to the west, in the Williston Basin, no Gamachian Fauna 13 has been recognized (Sweet 1979*b*; Barnes, unpublished collections from Manitoba), and the earliest Silurian conodonts compare well with those from the Manitoulin Formation of Ontario discussed by Barnes & Bolton (this volume). These conodont successions from the Midcontinent Region suggest that a major regression left the North American craton largely emerged for at least the duration of the Gamachian, and possibly longer, at least in some areas. The only exceptions to this, that is, areas where youngest Ordovician conodonts are present, are in marginal basins (e.g. Anticosti Island), some intracratonic troughs (e.g. in Arkansas–Missouri–Oklahoma; see Bergström & Boucot, this volume), outer miogeoclinal areas (e.g. Utah and Nevada), and regions having offshore basin and slope deposits (e.g. Gaspé and Arctic Canada).

In some Midcontinent areas (Fig. 2), incomplete stratigraphical successions produce intriguing conodont faunas of latest Ordovician age. Such faunas are known from the Cason Oolite of Arkansas (Craig 1969, 1986; Barrick 1986), the Noix Oolite and Girardeau Limestone of Missouri (Satterfield 1975; McCracken & Barnes 1982), and the Keel Formation of Oklahoma (Barrick 1986). These units yield sparse faunas characterized by *Noixodontus girardeauensis* (Satterfield). McCracken & Barnes (1982) assigned a Fauna 12 (Richmondian) age to the Noix fauna, but Barrick (1986) suggests that the presence of a *Hirnantia* fauna in several of these units indicates a latest Ordovician (late Gamachian, Hirnantian, Fauna 13) age. In the Yukon (Fig. 2), Lenz & McCracken (1982) recorded both *Noixodontus* and *Gamachignathus* in strata referred to the *Pacificograptus pacificus* Zone (the upper *Climacograptus supernus* Zone, equivalent to the lower part of the interval of the *Hirnantia* fauna in China; Lenz & McCracken 1982: fig. 6). In the Yukon, the overlying *Climacograptus extraordinarius* Zone is not recognized and that interval may be represented by a hiatus. The latest Ordovician *Glyptograptus persculptus* Zone is identified only with question, but significantly a Silurian conodont fauna is recorded from 6·3–13·3 m below the top of the *G. persculptus* Zone? in the Pat Lake section (Lenz & McCracken 1982, Appendix). With a hiatus below the *G. persculptus* Zone?, it is possible that only the uppermost part of that zone is present in the succession.

In the Canadian and Greenland Arctic regions, several conodont studies have been completed, or are under way, but little has been published to date. Preliminary results (Mayr *et al.* 1980) suggest the presence of a regionally developed hiatus in the systemic boundary interval. This is certainly the case in the carbonate platform facies (e.g., the Allen Bay Formation) and probably in the basinal facies as well, where the *G. persculptus* Zone has not been recognized.

Finally, Leatham (1985) has described a section in carbonate facies across the systemic boundary interval in the Great Basin. Absence of graptolites precludes recognition of the precise level of the systemic boundary. However, Leathan recognized an interval with mixed faunas between typical Ordovician and typical Silurian faunas, but he was inclined to believe that these mixed faunas were due to stratigraphical leaks or reworking of Ordovician conodonts into basal Silurian strata near an unconformity associated with the systemic boundary. In central Nevada, Ross *et al.* (1979) interpreted the Hanson Creek Formation as ranging without significant gap from the Late Ordovician to the Early Silurian. Fauna 13 seems to be represented in their collections but because they do not describe their Silurian conodonts, it is not clear how the conodont faunal succession is developed in the boundary interval.

Great Britain

No continuous section across the Ordovician–Silurian boundary developed in a facies suitable for conodont extraction is known from the British Isles. The boundary stratotype at Dob's Linn, Scotland (Fig. 2), as well as the lowermost part of the Llandovery reference standard in south Wales, are both unpromising for conodont work. A few conodonts have been recovered from shale bedding planes at the boundary stratotype, Dob's Linn (Barnes & Williams, this volume), and a single conodont collection is known from the lowermost Llandovery of the type area (Cocks *et al.* 1984). Efforts to collect from strata near the systemic boundary elsewhere in Britain have not been very successful; hence, only two productive samples are known from the Hirnantian (Bergström & Orchard 1985), none of them with very diagnostic species although the faunas are clearly of Ordovician aspect. Apparently, as in Scandinavia, the Hirnantian rocks in Britain are very poor in conodonts.

Currently available information about British early Llandovery conodonts derives largely from the work by Aldridge and co-workers. As noted by Aldridge (1985), very few conodonts are currently known from the Rhuddanian although a sample from the lower part of the stage at Llandovery contained a species association diagnostic of Aldridge's (1972) *Icriodella discreta–I. deflecta* Zone (Cocks *et al.* 1984). Aeronian strata in Wales and the Welsh Borderland have yielded taxonomically varied species associations (Aldridge 1985), which include *Kockelella*? *abrupta*, *Ozarkodina oldhamensis*, *O. hassi*, and *Pterospathodus*? *tenuis*. The upper Aeronian is characterized by the appearance of *Distomodus staurognathoides*, *Oulodus*? *fluegeli*, *Pseudooneotodus tricornis*, and *Kockelella ranuliformis*.The interval having this species association is referable to the *Distomodus staurognathoides* Zone (Aldridge 1972).

Scandinavia

The few sections in Sweden (Västergötland, Scania) and Denmark (Bornholm) where the base of the *Parakidograptus*? *acuminatus* Zone, and hence the base of the Silurian, can be recognized are all in dark shale facies from which no conodonts have been recovered. In other sections, shallow-water strata with the *Hirnantia* fauna (Bergström 1968) are overlain, in places unconformably, by Llandovery age shales and mudstones. In Sweden, the Ashgill conodont faunas are known from several sections (Bergström 1971*a*; Sweet & Bergström 1984) but the early Llandovery ones are virtually unknown. No conodonts have been recorded from the systemic boundary interval in Denmark.

Biostratigraphically well controlled lower Llandovery successions have recently been described from the Oslo region, Norway (Fig. 2). The conodont succession there is particularly significant because it can be tied to the distribution patterns of key graptolites and shelly fossils (Aldridge & Mohamed 1982). As is the case in Sweden, rocks of latest Ordovician (Hirnantian) age have produced very few conodonts, the only reasonably common species being a form close to, if not identical with, *Ozarkodina oldhamensis*, which is also characteristic of coeval strata in Sweden (Bergström 1971*a*: fig. 4:11). Absence of close graptolite control makes it impossible to establish the precise level of the systemic boundary in the Oslo region, but the graptolites indicative of the upper *Glyptograptus persculptus* Zone or lower *P.*? *acuminatus* Zone present in the lower Solvik Formation (Howe 1982) suggest that the systemic boundary is close to the base of that unit, which is separated from the underlying Hirnantian strata by what appears to be a minor gap. The recent suggestion that the appearance of the trilobite *Acernaspis* is coeval with the base of the *P.*? *acuminatus* Zone is not well supported by the conditions in the Oslo region where this genus makes it appearance in the middle Solvik Formation (6bα) in an interval that on graptolite evidence appears to be no older than the *Monograptus atavus* Zone (Howe 1982).

A summary of the conodont, shelly fossil, and graptolite biostratigraphy of the lower Llandovery of the Oslo region is given in Fig. 3. The faunal succession is quite similar to that of the Anticosti Island (Barnes & McCracken 1981; Lespérance 1985), Gaspé (Nowlan 1983; Lespérance 1985), and the Rhuddanian and lower Aeronian of Britain (Aldridge 1985; Cocks *et al.* 1984). In the lowermost Llandovery of the Oslo region, the presence of *Oulodus*? cf. *O.*? *nathani* strongly suggests that the *Oulodus*? *nathani* Zone can be recognized (Aldridge & Mohamed 1982), which is overlain by the *Distomodus kentuckyensis* Zone. In the uppermost part of the Solvik Formation, representatives of *Distomodus staurognathoides* and other species of the *D. staurognathoides* Zone make their entrance, which suggests correlation with the middle Aeronian of Britain (Aldridge 1975) and the lower part of the Jupiter Formation of Anticosti Island (Uyeno & Barnes 1983). Although the Llandovery conodont succession of the Oslo region is one of the best biostratigraphically controlled in the world, it unfortunately

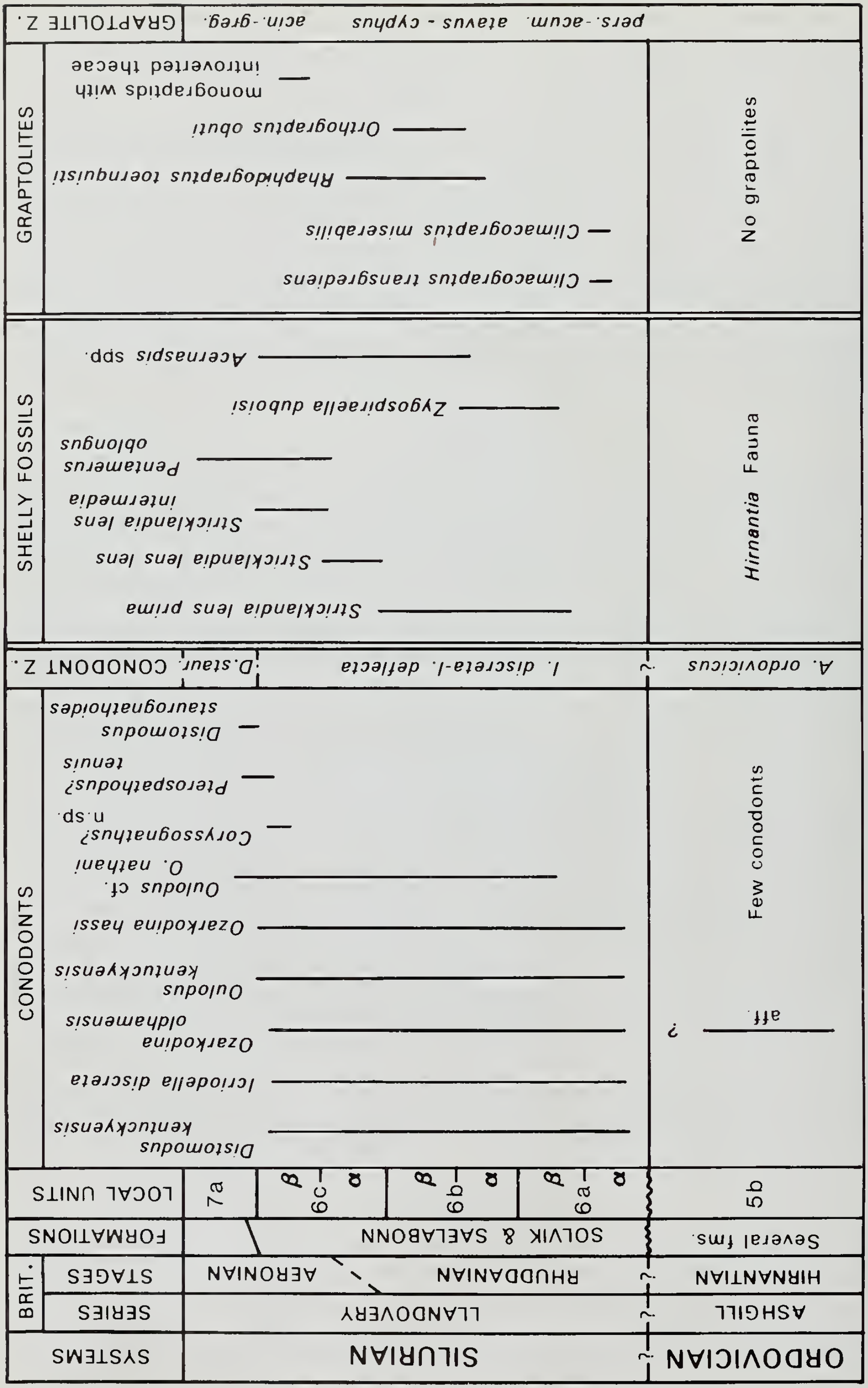

Fig. 3 Comparison of stratigraphical ranges of key conodonts, shelly fossils, graptolites, and conodont and graptolite zones in the lower Llandovery of the Oslo region, Norway. Based on many sources, particularly Howe (1982) and Aldridge & Mohamed (1982). Note that the *Hirnantia* fauna-bearing upper Ashgill (5b), which is separated from overlying rocks by a minor unconformity, has yielded only a few conodonts and no diagnostic graptolites.

provides little information about the conodont sequence right across the systemic boundary interval, despite the fact that much of this interval is developed in calcareous rocks that are readily digestible in weak acids.

Carnic Alps and nearby areas in Austria and Italy

The Cellon section in the Carnic Alps has become classic as the reference standard of much of the Silurian conodont zone succession (Walliser 1964) but this border region between Austria and Italy has several other important sections that include Late Ordovician as well as Early Silurian strata (Fig. 2) (Schönlaub 1969, 1971, 1979, 1980; Jaeger & Schönlaub 1977; Jaeger *et al.* 1975; Serpagli 1967; Vai 1971; Flajs & Schönlaub 1976). Because graptolites diagnostic of the *P.*? *acuminatus* Zone are unknown in the Carnic Alps, the precise level of the base of the Silurian cannot be determined in sections with more or less continuous sequence. In other sections, Silurian or younger strata rest unconformably on Ordovician beds and the systemic boundary coincides with a conspicuous stratigraphical gap.

Many of the conodont data available from this region pertaining to the Ordovician–Silurian boundary interval consist of lists of species, but there are also published descriptions and illustrations of Ashgill (Serpagli 1967; Flajs & Schönlaub 1976) and Llandovery (Walliser 1964; Schönlaub 1971) conodonts. Sweet & Bergström (1984) suggested some updating of the taxonomy of Ashgill species and additional taxonomic work on some of the faunas is clearly needed.

The most distinctive Ashgill age unit in the Carnic Alps is an argillaceous limestone a few metres thick, the Uggwa (Uqua) Limestone (= Tonflaserkalk). Although its conodont fauna, which was monographed by Serpagli (1967), includes some species currently unknown outside Austria and Italy, it is clearly of Ordovician rather than Silurian aspect and represents the *Amorphognathus ordovicicus* Zone. Some of its characteristic genera include *Amorphognathus*, *Ansella*, *Birksfeldia*, *Drepanoistodus*, *Hamarodus*, *Plectodina*, *Protopanderodus* and *Scabbardella*, which are all restricted to the Ordovician. In several sections, the Uggwa Limestone is followed by a prominent stratigraphical gap that may represent a portion of the Silurian (or more) and possibly also the uppermost Ordovician. At other sections, a part of this gap is filled by calcareous sandstones and dark shales, commonly referred to as the 'Untere Schichten', that locally, for instance at the Cellon section, contain megafossils of the *Hirnantia* fauna associated with Ashgill conodonts. Walliser (1964) classified the 'Untere Schichten' as the upper part of his Bereich 1 and referred this unit to the Lower Silurian. We believe that most, if not all, of the 'Untere Schichten' belongs to the uppermost Ordovician, if one follows the practice of having the systemic boundary at the base of the *P.*? *acuminatus* Zone.

As shown by Walliser (1964), the beds on the top of the 'Untere Schichten' at Cellon contain conodonts (*Apsidognathus tuberculatus*, *Distomodus staurognathoides* and *Pterospathodus celloni*) of the *P. celloni* Zone, and a similar fauna is known also from beds just above the Ashgill age limestone at the Mount Seewarte section (Schönlaub 1971, 1980). At both these sections, the stratigraphical hiatus associated with the systemic boundary includes two-thirds of the Llandovery (Rhuddanian and Aeronian stages). On the other hand, at other localities, such as the Feistritzgraben section (Jaeger *et al.* 1975; Schönlaub 1980), the Uggwa Limestone is directly overlain by dark shales that contain *Glyptograptus* cf. *G. persculptus* near their base. This suggests a much smaller, if any, stratigraphical gap above the limestone, and the systemic boundary is evidently at an unknown level in the clastic succession above the graptolite-bearing interval.

Although earliest Silurian, and perhaps also latest Ordovician, conodonts are unknown from the sections in the Carnic Alps and nearby regions, this area is of interest in discussions about the conodont biostratigraphy near the systemic boundary because of its rich Ashgill and middle and late Llandovery conodont faunas. Furthermore, in view of the local variations in both lithological and stratigraphical development near the systemic boundary, it is not excluded that further studies may lead to the discovery of stratigraphically more complete sections in a lithology suitable for extraction of conodonts than those now known.

Other areas

Outside North American and Europe, latest Ordovician and/or earliest Silurian conodonts are known from Siberia, China and Malaysia. In her review of the Ashgill conodont biostratigraphy of the Siberian Platform, Moskalenko (1983) recognized an *Aphelognathus pyramidalis* Zone in the topmost part (the Burian Stage) of the Ordovician but she noted that the succession is terminated by an erosional unconformity. Apart from the zonal index, the low-diversity and apparently largely endemic conodont fauna includes, among others, *Acanthodina nobilis*, *A. variabilis*, and *Acanthodus compositus* (Moskalenko 1973). Männik (1983) recorded a conodont succession through the Silurián of Severnaya Zemlya. The lowermost unit, the Vodopad Formation, yielded in its lower part *Ozarkodina oldhamensis*, *Icriodella* cf. *I. deflecta*, and *Oulodus*? cf. *O. kentuckyensis*, among others. This interval was referred to the *I. discreta–I. deflecta* Zone and interpreted to be of late Rhuddanian to early Aeronian (= Idwian in Männik) age. The similarity to coeval faunas in the Oslo region and eastern Canada is striking.

In China, the uppermost Ordovician, where present, is in most places developed in a lithology unsuitable for conodont extraction, and it has yielded only a few undiagnostic species (An 1981). Shelly facies of Llandovery age produce taxonomically varied and well preserved conodonts such as those from the Guizhou Province recorded by Zhou *et al.* (1981; also cf. Lin 1983) that provide correlation with the early Llandovery *I. discreta–I. deflecta* Zone, although some of the published identifications need confirmation.

Another section of interest in a discussion of the conodont biostratigraphy across the Ordovician–Silurian boundary is on Langkawi Islands, Malaysia (Igo & Koike 1967, 1968). The latest Ordovician and earliest Silurian are represented by clastic strata ('Lower Detritus Band'), but rocks below and above this interval have produced well-preserved conodonts. Although some of their identifications need reappraisal, it appears clear that the lowest Silurian fauna recorded by Igo & Koike (1968) represents the *Pterospathodus amorphognathoides* Zone and is of late Llandovery age (Fig. 1). A modern restudy of the Langkawi succession would be of considerable biostratigraphical interest.

Changes in conodont faunas across the Ordovician–Silurian boundary

One of the most striking, if not *the* most striking, faunal turnovers during the 400 million year long history of the Phylum Conodonta occurred near the Ordovician–Silurian boundary. As recently shown (Sweet 1985: figs 7, 8), the total species diversity decreased from an estimated 75–100 species in the lower-middle Ashgill (Sweet & Bergström 1984) to about 20 species in the lower Llandovery. This diversity reduction was not a sudden catastrophic event although only a few species survived into the Silurian; rather, during the Ashgill there was a gradual disappearance involving many characteristic and long-established stocks and the new taxa that appeared were considerably fewer than those that became extinct. However, within a very limited interval, probably in the latest Ashgill, most of the remaining Ordovician taxa were replaced by forms of Silurian aspect, producing a very different appearance of the conodont faunas. From both biostratigraphical and palaeobiological points of view, it is obviously of considerable interest to establish the precise timing and detailed scenario of the conodont faunal turnover. Unfortunately, conodont data from strata reliably dated as representing the *G. persculptus* Zone, and particularly the upper part of this zone, are few and incomplete, making it currently impossible to tie the turnover closely to the graptolite zone succession. As noted below, we believe that the turnover occurred before the beginning of the Silurian (as defined by the base of the *P.*? *acuminatus* Zone), but we admit that the evidence for this conclusion is not yet conclusive. The best illustration of the faunal turnover is in the Anticosti Island succession, where there seems to be no significant stratigraphical gap in the boundary interval. As described by McCracken & Barnes (1981), the Ordovician-type conodont fauna in the Hirnantian-age Ellis Bay Formation there includes some 38 species. Immediately above a thin (0·5–2 m thick) interval having a mixed fauna, there is a Silurian-type conodont fauna of about 21 species, 16 of which are not known from older strata. Because no graptolites useful for precise zonal classification are known from the turnover interval and the immediately overlying strata, this interval cannot yet be classified in terms of standard graptolite zones and even the base of the Silurian there cannot be tied to a specific stratigraphical level.

In Fig. 4 we illustrate the known ranges of significant conodont species in the Ashgill and lower Llandovery. It should be stressed that a compilation of this type, involving data from many different sources in widely different geographical regions, will necessarily be both incomplete and probably incorrect in some respects, especially as it is based partly on arbitrary age assessments of some faunas. One interesting feature emerging from Fig. 4 is that apparently, with the possible exception of a form in the still poorly known *Ozarkodina oldhamensis* complex, not a single species with compound elements in the apparatus survived the faunal turnover. Only a few generalized species of the coniform conodont genera *Dapsilodus*, *Decoriconus*, *Panderodus*, *Pseudooneotodus*, and *Walliserodus* range into the Lower Silurian, but it should be noted that the taxonomy of some of these taxa is still not very clear.

Figure 5 summarizes the known ranges of important genera in the Ashgill and lower Llandovery. Significantly, only eight of the more than 25 Late Ordovician genera range across the turnover interval. Among these, only three (*Icriodus*, *Oulodus*, and *Ozarkodina*) have compound elements in the apparatus, whereas the five other genera have apparatuses composed of exclusively coniform elements. In our interpretation, the *Amorphognathus* lineage, which may be traced back to the Early Ordovician (Bergström 1983), became extinct in the Hirnantian. In the past, some authors have referred the early Llandovery *Pterospathodus*? *tenuis* to *Amorphognathus*, presumably on the basis of a perceived similarity in the Pa elements. However, the ramiform elements of the apparatuses of the two genera differ markedly, and we question that the Silurian species has any affinity at all with *Amorphognathus*.

The mutual relations, and possibly synonomy, of the two Ashgill genera *Birksfieldia* and *Gamachignathus* are still unclear, and it is outside the scope of the present study to discuss those matters here. However, it should be noted that it is conceivable that the ancestor of the Silurian genus *Distomodus* is to be found among this group of Late Ordovician conodonts.

The *Icriodella* lineage can be traced, with no significant interruption, from the Llandeilo to the Ashgill (Bergström 1983). We are not aware of any confirmed record of the genus in the Hirnantian but several widely distributed species have been described from the Llandovery (Aldridge 1972). The platform elements in the Silurian species are certainly similar to those in the Ordovician forms, but the non-platform elements differ in some respects, and the relations between the Ordovician and Silurian forms referred to *Icriodella* need further study; it is premature to conclude that all these forms represent the same lineage.

The Late Ordovician and Early Silurian representatives of *Oulodus* exhibit close similarity in morphology (Sweet & Schönlaub 1975) and they appear to represent the same stock. The same applies to *Ozarkodina* but this genus is not well known from the Ordovician. Its stratigraphically oldest species, *O. pseudofissilis* from the upper *A. superbus* Zone (lower Ashgill) of Britain (Lindström 1959; Orchard 1980), is isolated stratigraphically from a Hirnantian species in Scandinavia close to *O. oldhamensis*. The latter is so close morphologically to Llandovery species of *Ozarkodina* that there appears to be no doubt that they represent the same lineage.

It may be significant that the genera that survived the turnover are widely distributed in Ordovician rocks, and the species involved may have been ecologically tolerant. Sweet & Bergström (1974: 20) noted that, when known, the ancestry of most Llandovery stocks appears to be from among forms with particularly wide distribution in Midcontinent (warm-water) Province Ordovician faunas, whereas the North Atlantic (cold-water) Province stocks virtually disappeared in the Late Ordovician. A possible exception may be *Dapsilodus*, which in the Ordovician is best known from, and most common in, North Atlantic Province faunas. The severe regression reduced the space and range of environments available to the Midcontinent faunas and presumably resulted in the demise of many stocks. Many coniform taxa seem to have been less affected, particularly forms interpreted as pelagic rather than nektobenthic in habit (e.g. McCracken & Barnes 1981). The North African glaciation would have created different oceanic conditions, in terms of circulation, oxygenation and cooler temperatures. This combination of factors probably reduced the diversity of late Ashgill conodont faunas and

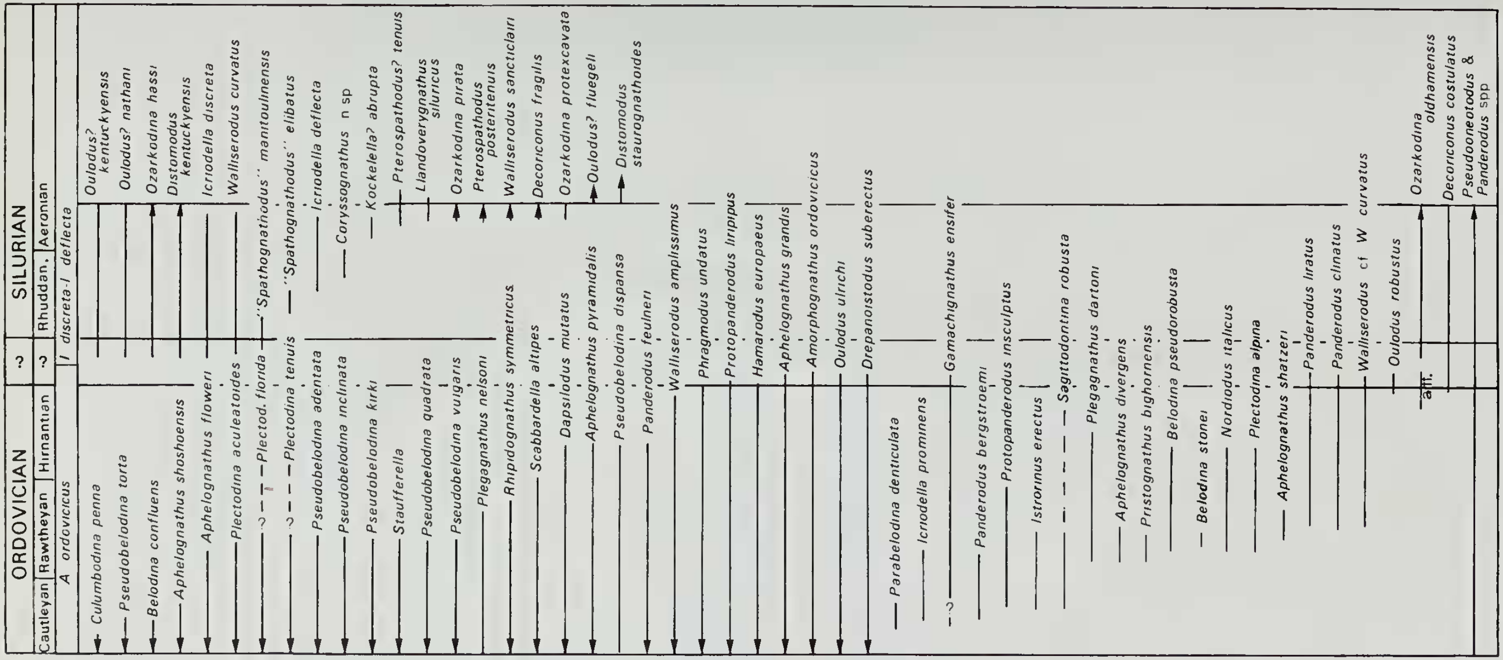

Fig. 4 Known ranges of 48 Ordovician-aspect and 22 Silurian-aspect conodont species in the uppermost Ordovician (Cautleyan to Hirnantian; *A. ordovicicus* Zone) and lowermost Silurian (Rhuddanian to lower Aeronian; *Icriodella discreta–I. deflecta* Zone). Because of uncertainties in correlations, especially in the Upper Ordovician and between continents, shown ranges are somewhat generalized. We estimate that the *A. ordovicicus* Zone contains an additional 25–50 named species that are so poorly known taxonomically and/or biostratigraphically that it is premature to include them in this diagram, and similarly a few species have been omitted from the *I. discreta–I. deflecta* Zone. Note the gradual species extinction, but also the appearance of new taxa, through the *A. ordovicicus* Zone, and the conspicuous faunal turnover in an interval near the systemic boundary.

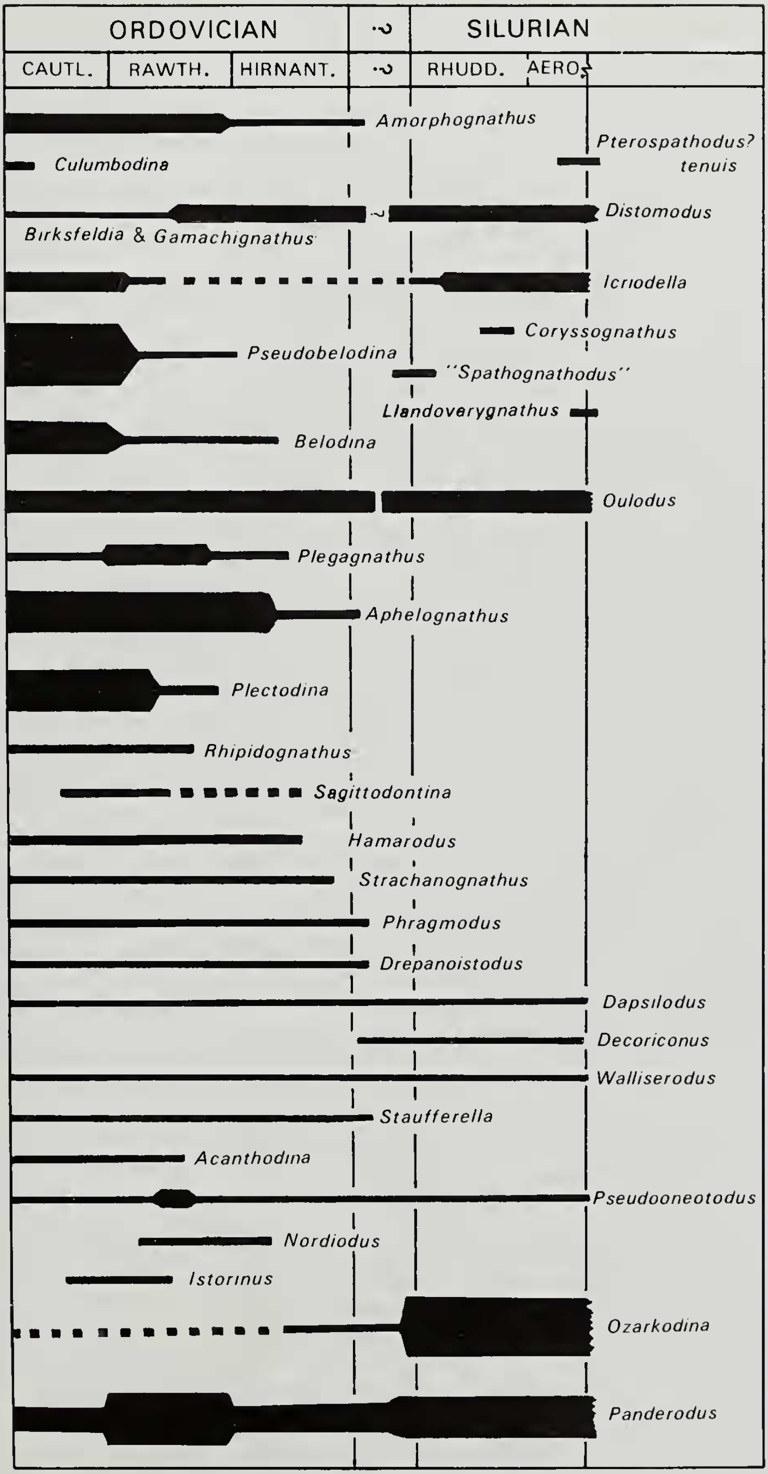

Fig. 5 Known ranges of important conodont genera in the *A. ordovicicus* and *I. discreta–I. deflecta* Zones. Relative width of vertical bars reflect number of species of a genus in a particular interval. Note that only eight of the 32 genera listed range across the systemic boundary interval, resulting in a very different generic composition of the faunas above and below.

produced the profound turnover (Barnes 1986). In addition, plate motions may have aided in these faunal changes since, by Hirnantian time, typical North Atlantic Province areas such as Baltica had moved into the tropical belt, which caused extinction of stocks long adapted to the conditions in high-latitude regions. If so, one would expect that perhaps some taxa of North Atlantic Province aspect would have survived into the Silurian in high-latitude regions, provided conditions did not become too severe. Unfortunately, high-latitude early Llandovery conodont faunas remain virtually unknown. Also, deeper-water early Silurian conodont faunas are poorly known, and it seems likely that the enigmatic origin of some of the Early Silurian platform genera may be discovered in such faunas.

Conodont Correlation of the Ordovician–Silurian boundary

As shown above, there is a profound conodont faunal change in the Ordovician–Silurian boundary interval. This faunal turnover occurs in both shallow-water cratonic and deep-water oceanic environments. The more detailed sampling and better faunal control that is feasible in carbonate platform successions is likely to provide more precise correlation within the boundary interval than can be expected in predominantly clastic deep-water oceanic deposits, which tend to contain fewer conodont-producing beds, and which are now largely preserved in structurally complex orogenic belts. Because diagnostic graptolites are largely restricted to the latter deposits, there is an obvious need to be able to recognize the systemic boundary accurately on the basis of fossils present in the cratonic successions. The geographically widespread and rapidly evolving conodonts can be expected to be helpful for precise correlations across facies boundaries also in the systemic boundary interval.

Three matters are of basic importance for the conodont correlation of the Ordovician–Silurian boundary: (1) the relation between the conodont faunal turnover and the systemic boundary in oceanic and slope sequences having zonal graptolites; (2) the relation between the conodont faunal turnover and the systemic boundary in platformal successions having key shelly fossils; and (3) if the conodont faunal turnover does not coincide with the graptolite-based systemic boundary, how do we define this boundary in terms of conodonts? All these matters involve several unsolved problems and, as will be shown below, we cannot now provide a definite answer to the last question.

In the North American platformal sequences, graptolites are rare or absent in the boundary interval. The informal units corresponding to Conodont Faunas 12 and 13, which are of Ashgill age (Fig. 1), have recently been replaced by a succession of formal conodont zones based on graphic correlation techniques (Sweet 1984: fig. 1), including the *Oulodus velicuspis*, *O. robustus*, *Aphelognathus grandis*, *A. divergens*, and *A. shatzeri* Zones. Latest Ordovician strata have a very restricted distribution on the North American craton due to a major regression associated with the Saharan glaciation(s). Further, the biostratigraphical, palaeoecological and biogeographical distributional constraints of latest Ordovician key taxa such as *Noixodontus* and *Gamachignathus* are not yet fully established. The interval of Faunas 12–13 corresponds broadly to the North Atlantic Province *Amorphognathus ordovicicus* Zone and also correlates with the lower Maysvillian to Gamachian stages, and the Cautleyan to Hirnantian stages (Fig. 1). On Anticosti Island as well as in Oklahoma–Arkansas–Missouri (Fig. 2), Gamachian cratonic faunas (Fauna 13) are associated with shelly faunas of *Hirnantia* fauna aspect. Available data show that this interval (that of Fauna 13) at least broadly correlates with the *Pacificograptus pacificus* and *Climacograptus extraordinarius* and at least part of the *Glyptograptus persculptus* Zones in the graptolite succession.

In the Yukon the first conodont faunas of Silurian aspect are found just below graptolites assigned to the *G. persculptus* Zone? (Lenz & McCracken 1982) in an interval possibly coeval with the upper part of this zone. If this interpretation is correct, it shows that the conodont faunal turnover was in latest Ordovician time and not coinciding with the systemic boundary. Lespérance (1985) has suggested that on Anticosti Island and Gaspé the level of appearance of *Acernaspis* is coeval with the base of the *P.*? *acuminatus* Zone, that is, the base of the Silurian. However, long-distance correlation of shelly fossils at the generic level is bound to be uncertain and the appearance of this trilobite in eastern Canada could obviously be younger than the base of the Silurian. On Anticosti Island, the level of the first appearance of *Acernaspis* is 30–70 m above the level of the first appearance of conodonts of Silurian aspect that mark the base of the *Oulodus*? *nathani* Zone. If the systemic boundary correlation of Lespérance (1985) is approximately correct, it is obvious that the horizon of the conodont faunal turnover is well below the base of the Silurian; it is certainly unlikely that it is higher than that stratigraphical level.

Some further data are available from other regions but unfortunately they are not decisive for establishment of the exact relationship between the conodont faunal turnover and the systemic boundary. Samples from the Carys Mills Formation of Maine and New Brunswick, possibly representing the *G. persculptus* Zone, contain faunas typical of the Silurian *Icriodella discreta–I. deflecta* Zone (Nowlan 1983; Bergström & Forbes unpublished). Conodonts of the *Amorphognathus ordovicicus* Zone are known from the *D. anceps* and *C. supernus* Zones at Dob's Linn, Scotland (Barnes & Williams, this volume) and Mirny Creek, northeast Siberia (Barnes, unpublished), respectively. Few sections are known where conodonts can be extracted from the *G. persculptus* Zone. At Mirny Creek, the basal *P.*? *acuminatus* Zone contains Silurian conodont faunas of the *I. discreta–I. deflecta* Zone, but the underlying *G. persculptus* Zone has not produced stratigraphically diagnostic conodonts (Barnes, unpublished).

We conclude that the precise correlation of the systemic boundary is uncertain in stratigraphically continuous shelly successions. Although a series of zones has been distinguished in graptolite-bearing successions, severe taxonomic problems involve several of the key species, and graptolite-based correlation into sequences with shelly fossils and conodonts is rarely possible, and conodont correlation into graptolitic facies is equally difficult. The degree of stratigraphical resolution appears greater for graptolites than for conodonts. However, Sweet's (1984) new zonal scheme for the North American Midcontinent has a resolution approaching that of the graptolite zone succession in China, and further refinements of the conodont zonal schemes are possible. If our suggestion that the conodont faunal turnover is in the upper *G. persculptus* Zone proves correct, the base of the Silurian, as now defined, will be above the interval of the most significant event in the conodont evolution of the Lower Palaeozoic. A future challenge is obviously to recover diagnostic conodonts from the *G. persculptus* Zone, and preferably from adjacent zones as well, in continuous sections, but very few sections suitable for this are known to us. In the meantime, a situation must prevail where the base of the *P.*? *acuminatus* Zone defines the base of the system in graptolitic successions, and the base of the *Oulodus*? *nathani* Zone defines a level *near* the systemic boundary in conodont sequences. Because of the prominent unconformity that is associated with the systemic boundary in most cratonic sequences, the latter level will in many, but not all, cases be the same as the systemic boundary. In stratigraphically more complete sections, it is possible that the difference between the graptolite-based boundary and the level of the conodont faunal turnover may correspond to as much as half a graptolite zone.

Conclusions

1. Although the conodont succession is known in considerable detail in both the Ashgill and the Llandovery, there are few data available from sections with rocks reliably dated by graptolites representing the upper *G. persculptus* and *P.*? *acuminatus* Zones.
2. Most boundary successions from which conodonts are known are stratigraphically incomplete or have intervals from which no diagnostic conodonts are known. The best known conodont succession across the boundary interval is on Anticosti Island, but the position of the graptolite-defined systemic boundary is uncertain there as the boundary interval lacks reliable graptolite control.
3. Ordovician and Silurian conodont faunas are strikingly different. The interval of faunal turnover is less than 2 m thick in the stratigraphically rather expanded section on Anticosti Island. The precise position, in terms of graptolite zones, of this turnover is still uncertain, but the available evidence indicates that it is likely to be in the upper part of the *G.*

persculptus Zone, below the systemic boundary. Hence it seems unlikely that the profound turnover coincides with the systemic boundary.

4. At the present time, the base of the *P.? acuminatus* Zone, that is the Ordovician–Silurian boundary, cannot be identified precisely on conodont evidence in sections with continuous sedimentation through the boundary interval. Further studies are needed in graptolite-controlled sections to clarify the exact relations between conodont and graptolite zones at the systemic boundary.

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